

NESTLING PROVISIONING RATES OF PEREGRINE FALCONS IN INTERIOR ALASKA

ANGELA G. PALMER,¹ DANA L. NORDMEYER,² AND DANIEL D. ROBY

USGS–Oregon Cooperative Fish and Wildlife Research Unit and Department of Fisheries and Wildlife, 104 Nash Hall,
Oregon State University, Corvallis, OR 97331 U.S.A.

ABSTRACT.—We examined factors influencing nestling provisioning rates among Peregrine Falcons (*Falco peregrinus*) breeding along the Tanana River, Alaska, in 1995–97. Perching birds (Passeriformes) composed the majority (54.3%) of prey delivered to the nests; whereas, ducks and grebes composed the majority of prey biomass (60.8%). After accounting for stage of the nesting cycle, delivery rates of prey items and estimated prey mass increased with brood size. Prey mass was positively correlated with the length of time an adult was absent from the vicinity of the nest prior to prey delivery. Finally, although we found that delivery rates of prey per nestling decreased with increasing brood size, estimated mass delivered per nestling did not vary with brood size. Peregrine Falcons apparently maintained constant provisioning rates per nestling as brood size increased by increasing prey mass.

KEY WORDS: *Peregrine Falcon; Falco peregrinus; foraging theory; Interior Alaska; nestling diet; nestling provisioning rates.*

TASAS DE APROVISIONAMIENTO A LOS POLLUELOS EN LOS HALCONES PEREGRINOS DEL INTERIOR DE ALASKA

RESUMEN.—Examinamos los factores que influyen las tasas de aprovisionamiento entre halcones peregrinos (*Falco peregrinus*) que se reprodujeron a lo largo del río Tanana, Alaska, en 1995–97. Los pájaros (Passeriformes) componen la mayoría (54.3%) de las presas entregadas en los nidos; mientras que, los patos y los zambullidores comprenden la mayoría de la biomasa de las presas (60.8%). Después de dar cuenta de la etapa del ciclo de anidamiento, las tasas de entrega de los ítem presa y la masa estimada de las presas incrementa con el tamaño de la nidada. La masa de la presa estuvo correlacionada positivamente con la longitud del tiempo en la que el adulto estuvo ausente de la vecindad del nido antes de la entrega de la presa. Finalmente, aunque encontramos que la tasa de entrega de presa por polluelo decreció con el aumento del tamaño de la nidada, la estimación de la masa entregada por polluelo no varió con el tamaño de la nidada. Los halcones peregrinos aparentemente mantuvieron constantes las tasas de aprovisionamiento por polluelo en nidadas que incrementaron su tamaño por medio del aumento del tamaño de las presas.

[Traducción de César Márquez]

Parent birds must provision nestlings adequately to ensure growth and survival of nidicolous young. Parents are limited in their ability to provide for nestlings by both environmental conditions and physiological constraints (Newton 1986), and parents confront a trade-off between investing in present versus future reproduction (Trivers 1972). Deerenberg et al. (1995) supported the existence of a trade-off between present and future reproduc-

tion by showing that daily energy expenditure of breeding Eurasian Kestrels (*Falco tinnunculus*) increased with artificially enhanced brood size, and was negatively correlated with subsequent survival of parents. In addition, although parents raising larger broods contribute more offspring to the population, the fitness of each fledgling from large broods may be lower than the fitness of fledglings from smaller broods (Dijkstra et al. 1990).

Lack (1954) and Gibb (1955) proposed that parent birds work as hard as they can to feed young, and that chicks from relatively larger broods are fed less than nestlings in average-sized broods. According to their hypothesis, provisioning rates per nestling should decline with a convex function as

¹ Present address: ABR, Inc., Environmental Research and Services, P.O. Box 240268, Anchorage, AK 99524 U.S.A.; e-mail address: apalmer@abrinc.com

² Present address: 5073 C Polaris Street, Eielson Air Force Base, AK 99702 U.S.A.

brood size increases. A survey of the literature on feeding frequencies of nestlings indicated that concave declines in feeding frequencies per nestling with increasing brood size are the norm, at least among passerines (Nur 1987). Among raptors, Newton (1986) found Eurasian Sparrowhawk (*Accipiter nisus*) prey-delivery rates were not influenced by the number of young in the nest; however, Masman et al. (1988) observed that male Eurasian Kestrels responded to experimentally increased hunger of broods by increasing active hunting.

Few studies have examined raptor provisioning rates and their relation to brood size. Enderson et al. (1972) found that larger Peregrine Falcon (*Falco peregrinus*) broods in Interior Alaska were fed more often, but individual nestlings in large broods received fewer feedings than small broods ($N = 7$ broods). White and Nelson (1991) documented the prey-delivery rate of one male peregrine to be approximately one prey item per hour. At 13 Peregrine Falcon nests in Australia, Olsen et al. (1998) observed that males provided more prey deliveries and more biomass to large broods than to broods of one or two chicks. We examined the relationships among Peregrine Falcon prey-delivery rate, prey size, mass-delivery rate, and brood size.

If Peregrine Falcon pairs were flexible in how they met food requirements of nestlings, we expected to find differences among pairs in prey-delivery rates and prey size in relation to brood size. We anticipated that mass-delivery rates (g/hr), a function of prey-delivery rates (items/hr) and prey size (g/item), would increase with increasing brood size.

Peregrine Falcons select a wide variety of predominantly avian prey species and sizes, and hunt over large local geographical areas (White and Nelson 1991, Ratcliffe 1993, Enderson and Craig 1997). They are thus good subjects for examining relationships between prey size and foraging time. We examined correlations between time away from the nest prior to a delivery and size of prey delivered.

Raising larger broods can produce more fledglings, but can be more energetically costly for parents (Deerenberg et al. 1995). We expected parents to deliver more food to larger broods, but because of the energetic costs of provisioning, pairs with larger broods would not be expected to provide as much food per nestling as pairs with smaller broods. Alternatively, if parents fully com-

pensated for each additional nestling in a brood, or if parents of higher individual quality produce larger broods, we would expect provisioning rates per nestling to be similar, regardless of brood size.

METHODS

Study Area. The study area encompassed a 250-km stretch of the Tanana River between Tok and Fairbanks, Alaska (from 63°8'N, 143°36'W–64°18'N, 148°45'W). In 1995, the study area extended from Tanacross to Sawmill, a 110-km stretch of river. In 1996 and 1997, we included an additional 65-km section of the river from Delta to Salcha. Observations were initiated each year after ice break-up in mid-May, and continued until the young had fledged and left the area of the nest in late-August to early-September. Two separate crews of 2–4 observers recorded data at nests.

Nests, which were situated on bluffs overlooking the river, were selected based on availability of accessible observation sites on gravel bars opposite cliffs with visibility of the nest ledge. To observe prey deliveries we established sites across at least one channel of the river and about 300 m from nests.

Provisioning Rates. Each field crew used binoculars, 15–60× spotting scopes, and a 90× Questar® (New Hope, PA) telescope to assist with observations. We kept the Questar trained on the nestlings or fledglings to aid our identification of prey deliveries. During the brood-rearing period, at least two (1995) or three (1996–97) observers recorded data. In all years, at least four observers recorded data during the post-fledging stage of the nesting cycle. Observations were performed during daylight hours.

We observed 10 breeding pairs in 1995, 9 breeding pairs in 1996, and 10 breeding pairs in 1997 from a total of 17 nest sites, where a nest site was defined as a nesting territory with a breeding pair (Steenhof 1987). Of these sites, we observed eight sites in one year only, six sites in two years, and three sites during all three years of the study. We made observations during the brood-rearing and post-fledging phases. Of the 10 breeding pairs observed in 1995, we observed all during brood-rearing and four during post-fledging periods. In 1996, we recorded provisioning rates from eight breeding pairs during brood-rearing period. One nest failed prior to fledging, we observed provisioning rates from the seven remaining pairs plus an additional pair during the post-fledging stage. In 1997, we observed all 10 breeding pairs during both brood-rearing and post-fledging. For analysis, we subdivided observations into four stages of the nesting cycle: early brood-rearing periods (0–10 d post-hatch), mid-brood-rearing (11–24 d), late brood-rearing (25 d until fledging), and post-fledging (ca. 40+ d) stages. We determined the stages of the brood-rearing phase during banding visits by estimating age of the oldest chick based on feather development and comparisons to Nelson's (1970) drawings of chicks. During early, mid, and late brood-rearing, and post-fledging stages, we made observations from 12, 14, 18, and 22 breeding pairs respectively (all years combined; Table 1).

For each breeding pair, we recorded the number of prey deliveries, the estimated size class of each prey item,

Table 1. Number of breeding Peregrine Falcon pairs observed by brood size during each stage of the nesting cycle along the Tanana River, Alaska 1995–97.

STAGE OF THE BREEDING CYCLE	BROOD SIZE				TOTAL
	1	2	3	4	
Early nestling-rearing	2 (9) ^a	2 (10)	5 (23)	3 (11)	12
Mid nestling-rearing	1 (5)	5 (29)	4 (15)	4 (17)	14
Late nestling-rearing	3 (6)	5 (23)	8 (27)	2 (8)	18
Post-fledging	4 (15)	9 (45)	5 (22)	4 (19)	22

^a (Total number of 4-hr observation sessions).

and the type of prey delivered (identified to finest taxon possible). To measure provisioning rates, we estimated the mass of those prey identified to species using mean body mass of that species (Burt and Grossenheider 1980, Dunning 1993). For prey identified only to genus or family, we used the mean mass of all the species of that genus or family (Dunning 1993) that regularly occurred in the study area, except in the case of shorebirds, which span a wide range of masses. We classified shorebirds and prey not identified to species, genus, or family into the following size classes: small (9–50 g), medium (51–200 g), large (201+ g), or unknown, to assign them an estimated mass. For both shorebirds and prey identified only to size-class, we used the median mass of all species of that size class known to regularly occur in the study area (30 g, 125 g, and 641 g for small, medium, and large items, respectively). We categorized prey of unknown size-class as medium-sized prey.

Peregrines sometimes delivered, cached, and redelivered prey items several times. In these instances, we counted the item as a single prey delivery. If part of a carcass (identified to species, genus, or family) was delivered, we assigned it the mass of that species, genus, or family, as outlined above. For unidentified partial carcasses we estimated the size of that item in relation to the size of the adult falcon and assigned it a size class of small (9–50 g), medium (51–200 g), or large (201+ g), based on the above methods of mass assignments.

For categorical analysis of prey size in relation to brood size, we only included those prey identified to species, genus or family, and classified items in small, medium, or large classes, based on the above methods of mass assignments.

Two video cameras, equipped with 250 mm lenses and 2× extenders, were employed to record prey deliveries continuously during observation sessions from observation sites. In 1995, we used Canon L2 Hi-8 mm (Canon, Inc., Tokyo, Japan) and Sony CCD-FX430 8 mm video cameras (Sony Corporation, Tokyo, Japan), and in 1996 and 1997 we used Canon L2 cameras. During the brood-rearing stage, one camera was focused on the nest ledge, while the other was focused on the attending adult. During the post-fledging stage, we focused on fledglings or adults as visibility allowed. Videotapes confirmed prey deliveries if observations were uncertain.

We estimated mass-delivery rates during each stage of the nesting cycle for each nest by averaging total mass delivered among 4-hr observation sessions. Similarly, we

calculated prey-delivery rates during each stage for each nest by averaging total number of prey delivered during 4-hr observation sessions. Finally, to estimate mean mass per session per nest per stage, we divided the total estimated mass of prey delivered by the total number of items delivered per 4-hr observation session, and then calculated the mean for the total number of observation sessions in that stage. During a given stage of the nesting cycle we conducted a mean of 4.0 (SD = 2.4) 4-hr observation sessions at a given nest, with a total of 284 observation sessions at all nests (Table 1). Observation sessions were sometimes back-to-back. We sampled provisioning rates from all daylight hours at each nest during each stage of the nesting cycle observed; however, observations at all nests were concentrated from 0800–1700 H Alaska Daylight Time. Observation sessions were excluded from analyses if poor visibility persisted throughout the session or, in the case of the post-fledging stage, when fledglings were not at the nest site. We treated nest sites independently among years.

We also examined the relationship between the length of time an adult was absent from the vicinity of the nest prior to a delivery (time away) and the estimated mass of the prey delivered. For this analysis, we excluded the first item of every observation session and included only prey identified to species, genus, or family.

For successful nests, mean brood size at fledging was 2.55 (SD = 1.0, range = 1–4 nestlings; Nordmeyer 1999), which was similar to mean brood size reported throughout Interior Alaska (Cade 1960, Ambrose et al. 1988, J Wright and P. Bente unpubl. data). Five nests had one chick, nine nests had two chicks, nine nests had three chicks, and six nests had four chicks. We observed four nests that experienced reductions in brood size prior to fledging: two broods from three to one chick, one brood from three to two chicks, and the fourth brood from four to three chicks.

Statistical Analyses. We used linear regression to assess the relationships of estimated number and mass of prey delivered and mean estimated prey mass as a function of brood size, and of estimated mass as a function of time away. We used Analysis of Variance (ANOVA) and Bonferroni's multiple comparison procedure to assess differences in provisioning rates among stages of the nesting period. We used lack-of-fit *F*-tests to test the adequacy of linear regression models versus separate means models for comparisons between provisioning rates and brood size. In the regression analyses we accounted for stage of

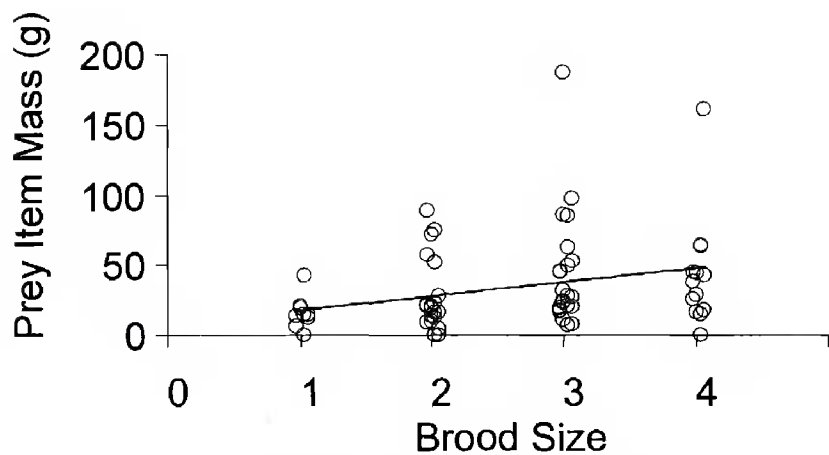


Figure 1. The relationship between prey item mass and brood size among Peregrine Falcons breeding along the Tanana River, Alaska, 1995–97. Prey item mass is presented as mean estimated prey item mass per nest per stage of the nesting period. The regression line is not adjusted for stage of the nesting period.

the nesting period and used weighted means based on the sample size of 4-hr observation blocks from each nest per stage, but we present unadjusted data in the figures. We log-transformed mass-delivery rates to meet the assumptions of the statistical tests. Additionally, we used a χ^2 test to examine the relationship between prey size-class and brood size. Means are reported as $\bar{x} \pm SE$.

RESULTS

Taxonomic Composition of Prey. Of the 343 prey observed delivered to nestlings, 201 (58.6%) could be identified to a taxonomic group. Most identified prey were passerines (Passeriformes; 54.3%), with shorebirds (Charadriiformes; 23.5%), ducks (Anatidae) and grebes (Podicipedidae; 13.0%), and gulls and terns (Laridae; 6.5%) comprising most of the remainder (Table 2). Ducks and grebes were the most important prey category in terms of biomass, comprising 60.8% of total estimated prey biomass. Shorebirds followed at 14.1%, gulls and terns at 9.7%, and passerines at 11.2% of total prey biomass. Small mammals were delivered on three occasions, and comprised an estimated 1.1% of prey biomass.

Prey Size. Of the 343 prey that we observed being delivered to young, 232 items (67.6%) were identified to a size category. Overall, more small items (126; 54.3%) were delivered than either medium (69; 29.7%) or large (37; 15.9%) items (χ^2_2 goodness of fit test = 52, $P < 0.001$). When prey of all size-categories were included, there was a trend towards a relationship between brood size and prey size class (χ^2_6 contingency test for independence = 11.14, $P = 0.08$), indicating that in general, parents with small broods deliver smaller items than parents with large broods. Additionally,

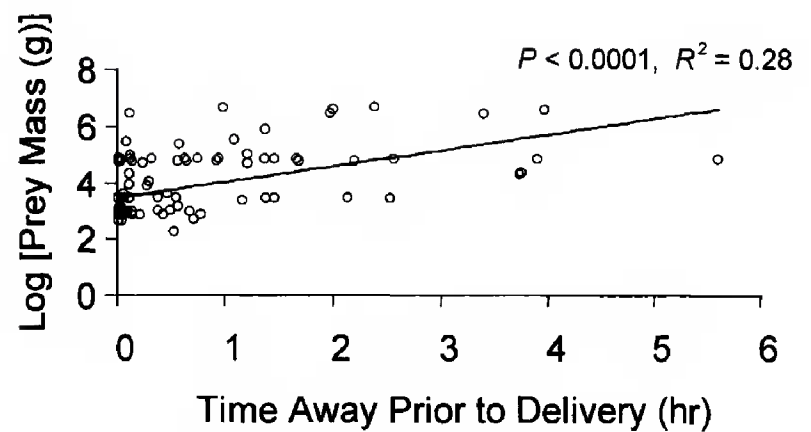


Figure 2. Log (estimated prey mass) as a function of time away from nest cliff prior to prey delivery for Peregrine Falcons nesting along the Tanana River, Alaska, 1995–97.

we noted a trend towards fewer medium-sized items brought to broods of two ($P = 0.11$, analysis of standardized residuals).

We found a positive relationship between prey mass and brood size ($P < 0.05$, $R^2 = 0.15$, $N = 66$). Median prey mass increased a mean of 24% ($\pm 10\%$) with each additional nestling (Fig. 1). Par-

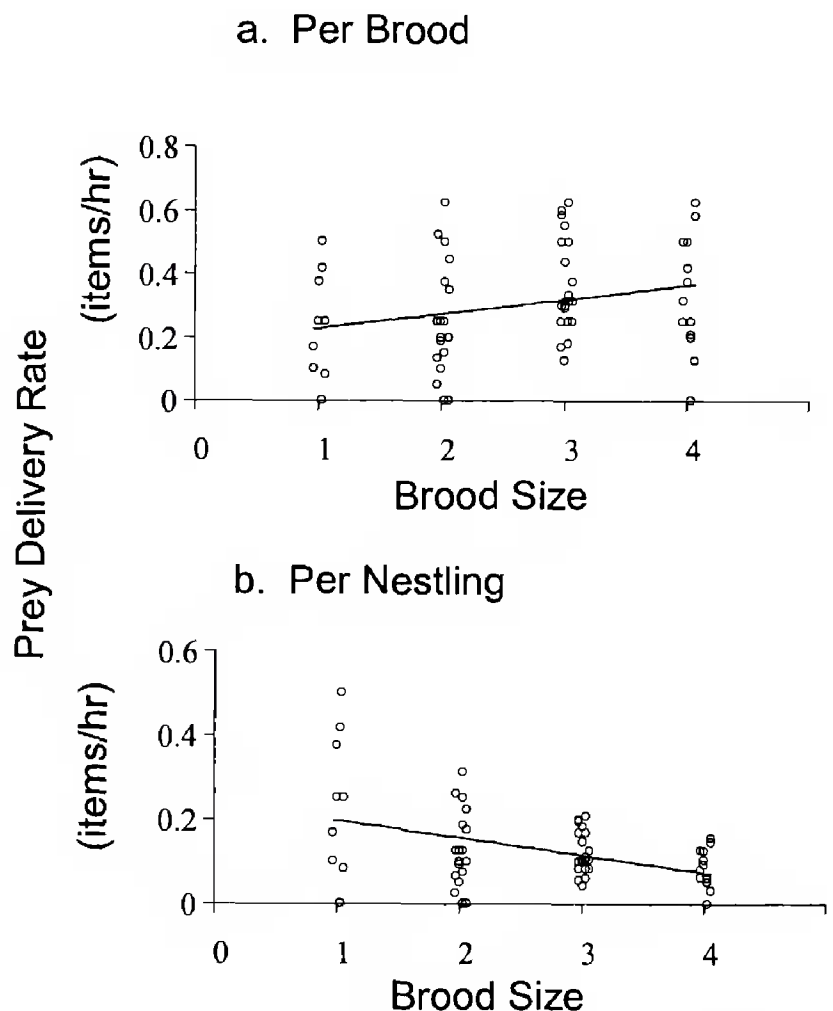


Figure 3. Mean prey delivery rates per brood (a) and per nestling (b) as a function of brood size in Peregrine Falcons nesting along the Tanana River, Alaska, 1995–97. The regression lines are not adjusted for stage of the nesting period.

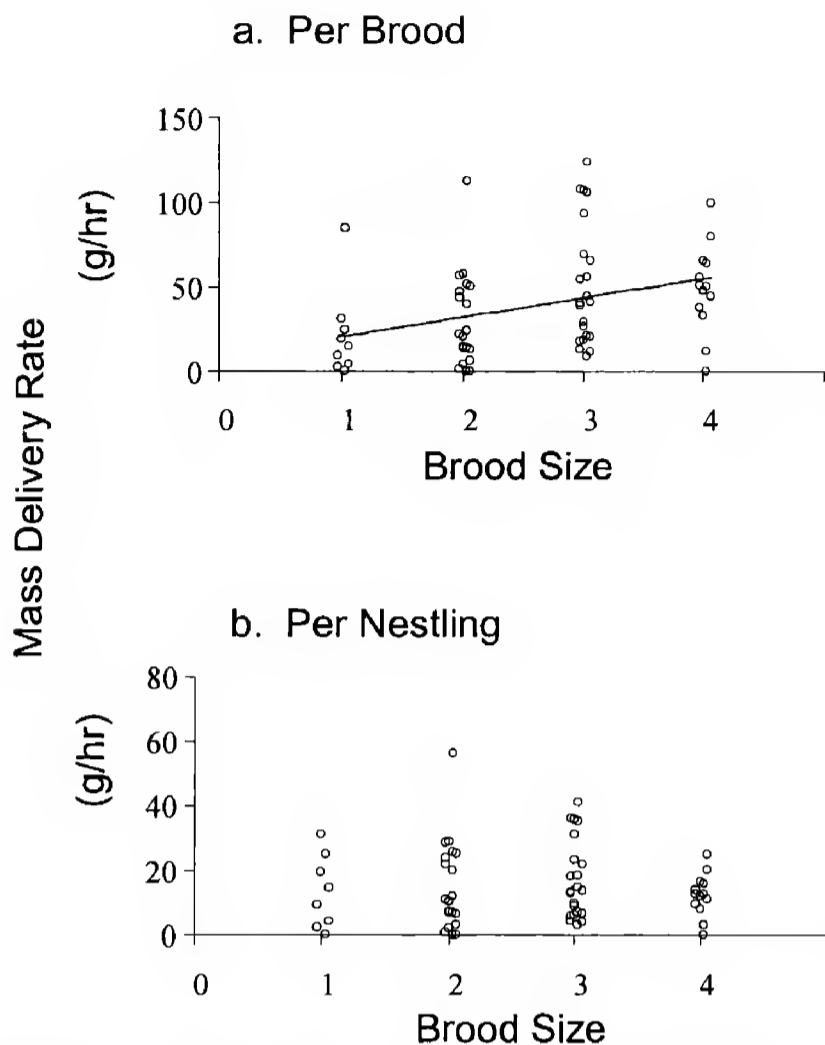


Figure 4. Mass-delivery rate per brood (a) and per nestling (b) as a function of brood size in Peregrine Falcons nesting along the Tanana River, Alaska, 1995–97. In (a) the regression line is not adjusted for stage of the nesting period. In (b) no linear relationship was evident per nestling.

ents of single-chick broods delivered no prey over 200 g, during 140 hr of observations and 31 deliveries, except for one delivery of a gull (*Larus* spp.; 308 g). Together with data on prey size, these analyses indicate that Peregrine Falcons maintained provisioning rates for larger broods by increasing mean prey size.

Time Away. There was a positive relationship between the time an adult was away from the nest area prior to a prey delivery (hr) and estimated mass of delivered prey (slope = 0.51 [$\log(\text{g}) \text{ hr}^{-1}$] ± 0.08 , $P < 0.001$, $R^2 = 0.29$, $N = 111$; Fig. 2). This is consistent with the inverse relationship between number of prey delivered and mean mass (slope = -2.09 ± 0.27 , $P < 0.001$, $R^2 = 65.8$, $N = 66$).

Stage of the Nesting Cycle and Prey-provisioning Rates. Prey-delivery rates did not differ among stages of the nesting period ($N = 66$, $P > 0.10$ for family-wise multiple comparisons). Prey mass and mass-delivery rates also did not differ among stages

of the nesting period ($F_{3,65} = 1.04$, $P > 0.3$; and $F_{3,65} = 1.19$, $P > 0.3$; respectively).

Brood Size and Prey-provisioning Rates. Brood size was positively related with both prey-delivery rate ($R^2 = 0.35$, $P = 0.002$, $N = 66$; Fig. 3a) and mass-delivery rate ($R^2 = 0.25$, $P = 0.02$, $N = 66$; Fig. 4a). Supporting these relationships, a positive linear relationship was suggested between both prey-delivery rates and mass-delivery rate versus brood size, (Lack-of-Fit F -tests were not significant: $P = 0.93$ and $P = 0.71$, respectively). Peregrine Falcons delivered a mean of 23% ($\pm 7\%$) more prey with each additional chick in the brood, and median mass-delivery rates increased 53% ($\pm 12\%$) with each additional chick.

Prey Provisioning Per Nestling. Prey-delivery rates per nestling declined with increasing brood size ($P = 0.001$, $R^2 = 37.7$, $N = 66$; Fig. 3b). In contrast, mass-delivery rates per nestling did not change appreciably with increasing brood size (Fig. 4b). Median prey-delivery rate per nestling declined 8% ($\pm 6\%$; Fig. 3b) with each additional nestling. In contrast, the slope of the regression of mass delivery rate per nestling on brood size did not differ from zero, after accounting for nesting stage (2-sided test, $P > 0.5$; Fig. 4b). This suggests that breeding pairs did not compensate for larger broods by proportionately increasing the rate of prey delivery, but instead increased the size of prey delivered.

DISCUSSION

Our results are consistent with the hypothesis that parents must work harder to provide for larger broods. Pairs with larger broods had higher prey-delivery rates (Fig. 3a), and higher mass-delivery rates (Fig. 4a). However, prey-delivery rates per nestling declined with increasing brood size, indicating that, by capturing proportionately more prey, parents did not fully compensate for larger broods (Fig. 3b). Additionally, we found no relationship between per nestling mass-delivery rates and brood size; the mass-delivery rate was constant across brood sizes (Fig. 4b). Prey-delivery rates per nestling declined with increasing brood sizes. Thus, to maintain constant mass-delivery rates per nestling across brood sizes, parents of larger broods must have compensated for lower prey-delivery rates per nestling by providing larger prey on average. In support of this interpretation, prey mass increased with brood size (Fig. 1), and parents of small broods rarely delivered large items.

Table 2. Frequencies of prey items observed and identified upon delivery to Peregrine Falcon nestlings at nests along the Tanana River, Alaska 1995-97

COMMON NAME (SCIENTIFIC NAME)	AGE/SEX	FRE- QUENCY	PERCENT OCCURRENCE	BODY MASS (g) ^a	PERCENT TOTAL PREY MASS
Grebe spp. (Red-necked or Horned) (<i>Podiceps</i> spp.)	—	3	1.5	738	8.3
Mallard (<i>Anas platyrhynchos</i>)	female	2	1.0	1082	8.1
American Wigeon (<i>Anas americana</i>)	female	1	0.5	719	2.7
American Wigeon (<i>Anas americana</i>)	male	2	1.0	792	6.0
Green-winged Teal (<i>Anas crecca</i>)	male	1	0.5	364	1.4
Green-winged Teal (<i>Anas crecca</i>)	—	2	1.0	340	2.6
Scaup spp. (Greater or Lesser) (<i>Aythya</i> spp.)	male	1	0.5	891	3.3
Duck spp. (Anatinae spp.)	female	1	0.5	722	2.7
Duck spp. (Anatinae spp.)	—	6	3.0	746	16.8
Duckling (Anatinae spp.)	Juvenile	4	2.0	30	0.5
Duck/grebe spp. (Anatinae spp. or <i>Podiceps</i> spp.)	—	3	1.5	745	8.4
Total ducks and grebes (Anatinae and Podicipidae)	—	26	13.0	—	60.8
Red-necked Phalarope (<i>Phalaropus lobatus</i>)	—	1	0.5	34	0.1
Least Sandpiper (<i>Calidris minutilla</i>)	—	2	1.0	23	0.2
Lesser Yellowlegs (<i>Tringa flavipes</i>)	—	7	3.5	81	2.1
Yellowlegs spp. (Greater or Lesser) (<i>T. flavipes</i> or <i>T. melanoleuca</i>)	—	5	2.5	126	2.4
Solitary Sandpiper (<i>Tringa solitaria</i>)	Juvenile	1	0.5	48	0.2
Upland Sandpiper (<i>Bartramia longicauda</i>)	—	1	0.5	150	0.6
Spotted Sandpiper (<i>Actitis macularia</i>)	—	10	5.0	32	1.2
Spotted Sandpiper (<i>Actitis macularia</i>)	—	3	1.5	32	0.4
Shorebird spp. (Scolopacidae spp.) small	—	3	1.5	30	0.3
Shorebird spp. (Scolopacidae spp.) medium	Juvenile	14	7.0	125	6.6
Total Shorebirds (Scolopacidae)	—	47	23.5	—	14.1
Mew Gull (<i>Larus canus</i>)	—	1	0.5	404	1.5
Bonaparte's Gull (<i>Larus philadelphia</i>)	—	1	0.5	212	0.8
Gull spp. (Mew or Bonaparte's (<i>Larus</i> spp.))	—	3	1.5	308	3.5
Gull nestling (<i>Larus</i> spp.)	Juvenile	2	1.0	125	0.9
Arctic Tern (<i>Sterna paradisaea</i>)	—	5	2.5	110	2.1
Gull/tern spp. (<i>Larus</i> spp. or <i>Sterna</i> spp.)	—	1	0.5	242	0.9
Total gulls and terns (Laridae or Sternidae)	—	13	6.5	—	9.7
Rock Dove (<i>Columba livia</i>)	—	1	0.5	355	1.3
Northern Flicker (<i>Colaptes auratus</i>)	—	1	0.5	142	0.5
Grouse spp. (<i>Bonasa umbellus</i> or <i>Dendragapus canadensis</i>)	—	1	0.5	337	1.3

Table 2. Continued.

COMMON NAME (SCIENTIFIC NAME)	AGE/SEX	FRE- QUENCY	PERCENT OCCURRENCE	BODY MASS (g) ^a	PERCENT TOTAL PREY MASS
Olive-sided Flycatcher (<i>Contopus cooperi</i>)	—	1	0.5	32	0.1
Bohemian Waxwing (<i>Bombycilla garrulus</i>)	—	1	0.5	56	0.2
Black-billed Magpie (<i>Pica pica</i>)	—	2	1.0	178	1.3
Gray Jay (<i>Perisoreus canadensis</i>)	—	4	2.0	73	1.1
Gray Jay (<i>Perisoreus canadensis</i>)	Juvenile	1	0.5	73	0.3
Dark-eyed Junco (<i>Junco hyemalis</i>)	—	8	4.0	20	0.6
Cliff Swallow (<i>Petrochelidon pyrrhonota</i>)	—	1	0.5	22	0.1
Violet-green Swallow (<i>Tachycineta thalassina</i>)	—	6	3.0	14	0.3
Violet-green Swallow (<i>Tachycineta thalassina</i>)	Juvenile	1	0.5	14	0.1
Bank Swallow (<i>Riparia riparia</i>)	—	1	0.5	15	0.1
Tree Swallow/Violet-green Swallow (<i>T. bicolor</i> or <i>T. thalassina</i>)	—	2	1.0	17	0.1
Swallow spp. (Cliff, Tree, Violet-green, or Bank) (Hirundinidae)	—	45	22.4	18	3.0
Swallow spp. (Hirundinidae spp.)	Juvenile	6	3.0	18	0.4
Yellow Warbler (<i>Dendroica petechia</i>)	—	1	0.5	10	0.1
Black-capped Chickadee (<i>Parus atricapillus</i>)	—	2	1.0	11	0.1
Townsend's Solitaire (<i>Myadestes townsendi</i>)	—	1	0.5	34	0.1
Swainson's Thrush (<i>Catharus ustulatus</i>)	—	1	0.5	31	0.1
Varied Thrush (<i>Ixoreus naevius</i>)	—	1	0.5	77	0.3
American Robin (<i>Turdus migratorius</i>)	—	1	0.5	77	0.3
Thrush spp. (Gray-checked, Swainson's, or Hermit) (<i>Catharus</i> spp.)	—	1	0.5	32	0.1
Small passerine spp. (Passeriformes spp.)	—	22	10.9	30	2.5
Total perching birds (Passeriformes)	—	109	54.3	—	11.2
Unknown avian spp.	—	142	—	—	—
Red Squirrel (<i>Tamiasciurus hudsonicus</i>)	—	1	0.5	240	0.9
Small rodent (Rodentia)	—	2	1.0	30	0.2
Total small mammal	—	3	1.5	—	1.1
Total	—	(343)	201 = 100%	26 616	g = 100%

^a We estimated prey mass using the mean body mass of that species (Dunning 1993). For prey identified to genus or family, we used the mean mass of all the species of that genus or family (Dunning 1993) that regularly occur in the study area, except in the case of shorebirds, which span a wide range of masses. We classified shorebirds into small (9–50 g) or medium (51–200 g) size classes based on estimated size in the field and assigned them the median mass of all species of that size class known to regularly occur in the study area (30 g and 125 g, respectively). We estimated mammalian prey masses from Burt and Grossenheider (1980).

Thus, different brood sizes seemed to be associated with different parental foraging strategies.

Time away from the nest prior to a delivery and size of prey were positively correlated (Fig. 2). Several variables can affect the time required for successful capture and delivery of prey of various sizes, such as hunger level of brood (Tinbergen and Drent 1980, Steidl and Anthony 2000), prey availability and distribution (Hunter et al. 1988, Meese and Fuller 1989, Rosenfield et al. 1995, Hakkarainen et al. 1997), prey handling time (Beissinger 1983), foraging efficiency (Winkler and Allen 1995, Bennetts and McClelland 1997), weather conditions (Steidl 1995), or distance traveled from the nest (Schoener 1979).

Cost of reproduction theory suggests that raising the maximum possible number of young causes reductions in parental survival, and thus, natural brood sizes are lower than maximum to optimize future survival and maximize lifetime reproductive output of adults (Dijkstra et al. 1990). Indeed, Nelson's (1988) observation that Peregrine Falcons more often failed to return to nest territories after rearing broods of three or four than after rearing broods of zero to two chicks suggests a cost to adults of raising larger broods. Also, Deerenberg et al. (1995) demonstrated a direct relationship between increased individual work-rate in parents with experimentally enlarged broods and local survival rate among adult Eurasian Kestrels. They proposed that an optimal work-rate might be a proximate control mechanism for brood size, because high work-rates may entail physiological weakening, leading to lower survival rates of breeders. Tolonen and Korpimäki (1996) suggest that parental effort (time spent flight hunting/total time) among Eurasian Kestrels is adjusted to the level where parental survival is not jeopardized, based on their evidence that males did not change parental effort in response to brood size manipulation, and females made only minor changes.

Mass-delivery rates per nestling, unlike per nestling prey-delivery rates, were constant across the range of brood sizes observed in this study. One possible explanation for constant mass-delivery rates per nestling, regardless of brood size, is that parents of smaller broods were working far below maximum sustained working capacity (Dijkstra et al. 1990, Stearns 1992). This could be because prey were readily available and easy to acquire. An alternative explanation is that pairs with larger

broods were better providers and able to regularly kill larger prey and transport it to the nest.

To raise large broods, parents must be efficient hunters to capture and deliver prey at adequate provisioning rates, and they need to maintain a work rate that does not impinge excessively on their future survival, and thus, reduce lifetime reproductive output (Deerenberg et al. 1995). If natural brood size is an indication of optimal workload per pair, then brood size may reflect parental foraging efficiency. In general, we observed more prey and larger prey delivered to larger broods. Larger prey were related to longer periods away from the nest area prior to delivery. In natural broods, we found parents had equal mass-delivery rates per nestling regardless of brood size, presumably maximizing both their present and future reproductive output. In our study, we were not able to evaluate the influence of age and breeding experience, which could be important factors on brood size and provisioning patterns. In future studies, distinguishing between parental hunting efficiency and prey availability will be essential to test foraging theory as it relates to provisioning of Peregrine Falcon young.

ACKNOWLEDGMENTS

Many people contributed to successful completion of this project. Major Robert Kull and Captain M. Carter directed funds from the Strategic Environmental Research and Development Program of the U.S. Department of Defense through the U.S. Air Force. Peter Bente (Alaska Dept. of Fish and Game (ADFG)) readily shared his extensive knowledge and experience about Peregrine Falcons and the Tanana River. Skip Ambrose (U.S. Fish and Wildlife Service), and Bob Ritchie and Steve Murphy (ABR, Inc.) offered important information and recommendations regarding the study design, literature, and fieldwork. ABR, Inc. also provided partial funds for publication preparation. Mike Collopy, Dan Schaffer, and Jerry Wolfe (Oregon State University) gave valuable advice. Bob Schults, Bob Fry, and Hank Tim of the Tetlin National Wildlife Refuge donated time and equipment, and Steve Debois and Dave Davenport of Delta ADFG, and Craig Gardner and Karen Ogden of Tok ADFG provided logistical support. Dave Yokel of the U.S. Bureau of Land Management loaned a Questar telescope during one year of the study. Norma Mosso, Judy Romans, Kathy Pearse, and Joy Huber of the USGS-Alaska Cooperative Fish and Wildlife Research Unit and Department of Biology and Wildlife, University of Alaska-Fairbanks, and others from the USGS-Oregon Cooperative Fish and Wildlife Research Unit and Department of Fisheries and Wildlife, Oregon State University provided technical support. The project would not have been possible without the dedicated observations by field assistants: Kurt and Nicole Lockwood, Steve Bethune, John Shook, Matt Kopec, Car-

men Thomas, Renee Crane, Nate Chelgren, Paul Berry, Dan Cariveau, Gwylim Blackburn, David Freed, Jay Kolbe, Jochen Mueller, and Jesse Bopp. We extend many thanks to Julian Fischer, Bob Steidl, and Carol McIntyre for their careful review of earlier versions of this manuscript. Referees Geoff Holroyd, Wayne Nelson, and Ted Swem provided thorough reviews and helpful insight making the manuscript a better paper.

LITERATURE CITED

- AMBROSE, R.E., R.J. RITCHIE, C.M. WHITE, P.F. SCHEMPF, T. SWEM, AND R. DITTRICK. 1988. Changes in the status of Peregrine Falcon populations in Alaska. Pages 73–82 in T.J. Cade, J.H. Enderson, C.G. Thelander, and C.M. White [EDS.], *Peregrine Falcon populations: their management and recovery*. The Peregrine Fund, Inc., Boise, ID U.S.A.
- BEISSINGER, S.R. 1983. Hunting behavior, prey selection, and energetics of Snail Kites in Guyana: consumer choice by a specialist. *Auk* 100:84–92.
- BENNETTS, R.E. AND B.R. MCCLELLAND. 1997. Influence of age and prey availability on Bald Eagle foraging behavior at Glacier National Park, Montana. *Wilson Bull.* 109:393–409.
- BURT, W.H. AND R.P. GROSSENHEIDER. 1980. A field guide to the mammals, 3rd Ed. The Peterson Field Guide series. Houghton Mifflin, New York, NY U.S.A.
- CADE, T.J. 1960. Ecology of the peregrine and Gyrfalcon populations in Alaska. *Univ. Calif. Publ. Zool.* 63:151–290.
- DEERENBERG, C., I. PEN, C. DIJKSTRA, B. ARKIES, F.H. VISER, AND S. DAAN. 1995. Parental energy expenditure in relation to manipulated brood size in the European Kestrel *Falco tinnunculus*. *Zoology* 99:39–48.
- DIJKSTRA, C., A. BULT, S. BIJLSMA, S. DAAN, T. MEIJER, AND M. ZIJLSTRA. 1990. Brood size manipulations in the kestrel (*Falco tinnunculus*): effects on offspring and parental survival. *J. Anim. Ecol.* 59:269–285.
- DUNNING, J.B., JR. (ED.). 1993. CRC handbook of avian body masses. CRC Press, Boca Raton, FL U.S.A.
- ENDERSON, J.H., S.A. TEMPLE, AND L.G. SWARTZ. 1972. Time-lapse photographic records of nesting Peregrine Falcons. *Living Bird* 11:113–128.
- AND G.R. CRAIG. 1997. Wide ranging by nesting Peregrine Falcons (*Falco peregrinus*) determined by radiotelemetry. *J. Raptor Res.* 31:333–338.
- GIBB, J.A. 1955. Feeding rates of Great Tits. *Br. Birds* 48: 49–58.
- HAKKARAINEN, H., V. KOIVUNEN, AND E. KORPIMÄKI. 1997. Reproductive success and parental effort of Tengmalm's Owls: effects of spatial and temporal variation in habitat quality. *Ecoscience* 4:35–42.
- HUNTER, R.E., J.A. CRAWFORD, AND R.E. AMBROSE. 1988. Prey selection by Peregrine Falcons during the nestling stage. *J. Wildl. Manage.* 52:730–736.
- LACK, D. 1954. The natural regulation of animal numbers. Clarendon, Oxford, U.K.
- MASMAN, D., S. DAAN, AND C. DIJKSTRA. 1988. Time allocation in the kestrel (*Falco tinnunculus*) and the principle of energy minimization. *J. Anim. Ecol.* 57:411–432.
- MEESE, R.J. AND M.R. FULLER. 1989. Distribution and behaviour of passerines around peregrine *Falco peregrinus* eyries in western Greenland. *Ibis* 131:27–32.
- NELSON, R.W. 1970. Some aspects of the breeding behaviour of Peregrine Falcons on Langara Island, B.C. M.S. thesis, University of Calgary, Calgary, Alberta, Canada.
- . 1988. Do large natural broods increase mortality of parent Peregrine Falcons? Pages 719–728 in T.J. Cade, J.H. Enderson, C.G. Thelander, and C.M. White [EDS.], *Peregrine Falcon populations: their management and recovery*. The Peregrine Fund, Inc., Boise, ID U.S.A.
- NEWTON, I. 1986. The sparrowhawk. T. & A.D. Poyser, Calton, U.K.
- NORDMEYER, D.L. 1999. Effects of jet aircraft overflights and other potential disturbances on behavioral responses and productivity of nesting Peregrine Falcons. M.S. thesis, Oregon State University, Corvallis, OR U.S.A.
- NUR, N. 1987. Parents, nestlings and feeding frequency: a model of optimal parental investment and implications for avian reproductive strategies. Pages 457–476 in A.C. Kamil, J.R. Krebs, and H.R. Pulliam [EDS.], *Foraging behavior*. Plenum Press, New York, NY U.S.A.
- OLSEN, P., V. DOYLE, AND M. BOULET. 1998. Variation in male provisioning in relation to brood size of Peregrine Falcons *Falco peregrinus*. *Emu* 98:297–304.
- RATCLIFFE, D. 1993. The Peregrine Falcon. T. & A.D. Poyser, London, U.K.
- ROSENFELD, R.N., J.W. SCHNEIDER, J.M. PAPP, AND W.S. SEEGAR. 1995. Prey of Peregrine Falcons breeding in West Greenland. *Condor* 97:763–770.
- SCHOENER, T.W. 1979. Generality of the size-distance relation in models of optimal foraging. *Am. Nat.* 114: 902–914.
- STEENHOF, K. 1987. Raptor management techniques manual assessing raptor reproductive success and productivity. Pages 157–170 in B. Pendleton et al. [EDS.], *National Wildlife Federation, Scientific and Technical Series No. 10*.
- STEARNS, S.C. 1992. The evolution of life histories. Oxford University Press, New York, NY U.S.A.
- STEIDL, R.J. 1995. Recreation and Bald Eagle ecology on the Gulkana National Wild River, Alaska. Ph.D. dissertation, Oregon Coop. Wildl. Res. Unit, Oregon State University, Corvallis, OR U.S.A.
- AND R.G. ANTHONY 2000. Experimental effects of human activity on breeding Bald Eagles. *Ecol. Appl.* 10: 258–268.
- TINBERGEN, J.M. AND R.H. DRENT. 1980. The starling as a successful forager. Pages 83–97 in E.N. Wright, I.R. Inglis, and C.J. Feare [EDS.], *Bird problems in agri-*

- culture. British Crop Protection Council, London, U.K.
- TOLONEN, P. AND E. KORPIMÄKI. 1996. Do kestrels adjust their parental effort to current or future benefit in a temporally varying environment? *Ecoscience* 3:165–172.
- TRIVERS, R.L. 1972. Parental investment and sexual selection. Pages 136–179 in G. Campbell [Ed.], *Sexual selection and the descent of man*. Aldine, Chicago, IL U.S.A.
- WHITE, C.M. AND R.W. NELSON. 1991. Hunting range and strategies in a tundra breeding peregrine and Gyrfalcon observed from a helicopter. *J. Raptor Res.* 25:49–62.
- WINKLER, D.W. AND P.E. ALLEN. 1995. Effects of handicapping on female condition and reproduction in Tree Swallows (*Tachycineta bicolor*). *Auk* 112:737–747.

Received 15 January 2002; accepted 20 September 2003
Former Associate Editor: Troy Wellicome